Deep-Diving California Sea Lions: Are They Pushing Their Physiological Limit?

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LONG-TERM GOALS

The 500-m diving capacity of the California sea lion (*Zalophus californianus*) represents a model in which a generally considered shallow-diving species is potentially approaching its physiological limit during dives greater than 300 m in depth. The physiology of these extreme dives is relevant to the development of the sea lion as a model for deep-diving physiology and to the performance and training of California sea lions used as part of the U.S. Navy's Marine Mammal Program. In addition, the limits of a species' physiological response to diving, especially during extreme dives, is key to understanding how the animal may respond to disturbances in the environment (i.e., sound, temperature, prey availability). In this study we will determine the rate and magnitude of O_2 store depletion during dives, and investigate its relationship to heart rate and workload, thereby improving our understanding of O_2 management during diving, specifically the role of lung O_2 stores and O_2 delivery to tissues.

OBJECTIVES

This study will utilize backpack digital recorders to measure blood oxygen depletion, heart rate, and flipper stroke rate in dives of California sea lions during maternal foraging trips to sea from San Nicolas Island. The goals of this research are 1) determination of the rate, pattern and magnitude of blood O_2 store depletion during both shallow and deep dives at sea, 2) documentation of heart rate profiles of shallow and deep dives, and assessment of the relationship between changes in heart rate to blood O_2 profiles, and 3) documentation of flipper stroke rate profiles during shallow and deep dives, and assessment of the relationship of stroke rate to both changes in heart rate and changes in blood O_2 profiles.

APPROACH

Objective 1: In order to calculate the rate and magnitude of depletion of the blood O_2 store during dives, arterial P_{O2} profiles will be obtained from a P_{O2} recorder and intravascular electrode deployed on sea lions. Venous P_{O2} profiles have already been collected in the PI's current ONR project with

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California sea lions. As in previous research by the PI with California sea lions and other species (Meir et al. 2009; Meir and Ponganis 2009), the P_{O2} profiles will be converted to Hb saturation profiles with the use of the sea lion O_2-Hb dissociation curve determined in the PI's current ONR project. In addition to the P_{O2} and Hb saturation profile during a dive, the start-of-dive and end-of-dive % Hb saturations can then be used to calculate the magnitude of blood O_2 depletion during dives based on the net change in % Hb saturation, and the known Hb concentration and blood volume.

Objective 2: ECG profiles will be collected from a second group of freely diving lactating female sea lions. The following indices of heart rate during dives will be measured and compared in shallow vs. deep dives: a) dive heart rate (total number of beats / dive duration), b) maximum heart rate during a dive, c) minimum heart rate, d) time into the dive (% of dive duration) until resting heart rate (70 bpm) (Ponganis et al. 1997) is reached, and e) duration of and heart rate during the ascent tachycardia. If possible, heart rate during rest periods will also be measured if females are seen resting on land. Although heart rate will not be measured concurrently with P_{O2} we will compare heart rate and P_{O2} data between dives of similar duration and depth to determine any potential relationship between heart rate and blood O_2 depletion.

Objective 3: Accelerometers will be deployed on females with ECG data loggers in order to evaluate stroke-glide patterns in shallow vs. deep dives and to examine the relationship between heart rate and stroke rate. Although venous P_{O2} will not be measured concurrently with stroke rate, we will compare stroke rate and venous P_{O2} depletion profiles (collected for our previous ONR funded project) between dives of similar duration and depth to determine any potential similarities between stroke rate and venous blood O_2 depletion rate profiles. In addition, we will evaluate whether there is any difference in the relationship of stroke rate vs. venous O_2 depletion in shallow vs. deep dives.

WORK COMPLETED

The second field season is underway as this report is being written. In the first season, deployment of ECG recorders and accelerometers allowed collection of data from 461 dives in five sea lions. Dives were as deep as 420 meters and ranged from one minute to 10 minutes in duration. Dive duration correlated highly with maximum depth of dive. Preparation of manuscripts for publication and talks for presentation at the upcoming Marine Mammal Conference are in progress.

RESULTS

Heart rate data have been almost completely anlayzed, and will be reviewed subsequently. Accelerometer data analysis is in progress, but initial review indicates that during deep dives, after initial stroking for 30 seconds, the sea lions primarily glide during descent to depths of 350 to 400 meters, and then gradually stroke at the bottom of the dive and during ascent (Fig. 1). Resting heart rates were 54 $\pm$ 6 beats min^{-1} (bpm), and in dives of 1-3 min, 3-5 min, and > 5 min, dive heart rates (number of beats/dive duration) were 55 $\pm$ 8, 51 $\pm$ 6, and 40 $\pm$ bpm. As illustrated in Figs. 1 and 2, the heart rate profile was characterized by rapid development of a bradycardia (slow heart rate), and a gradual increase in heart rate during the bottom phase of the dive and during ascent. The degree of bradycardia was more intense in deeper dives with heart rates as low as 10 bpm during the deepest dives.

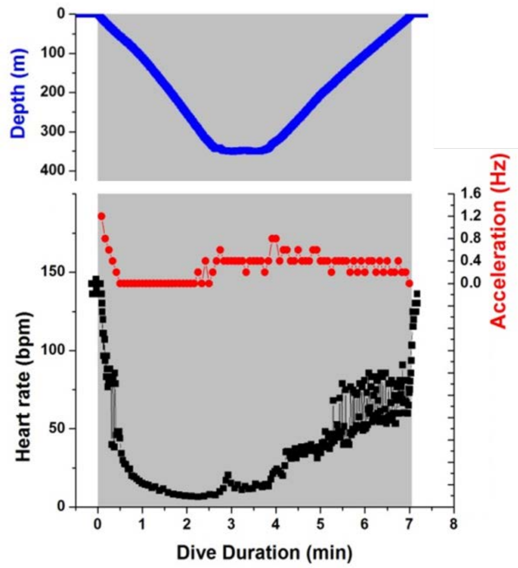

Figure 1. Heart rate (beats per min (bpm)) and stroke rate (acceleration axis in Hertz (Hz)) during a 350-m deep dive of a California sea lion. Note that stroke rate declines to zero by 30 s into the dive and that heart rate reaches 10 bpm in late descent.

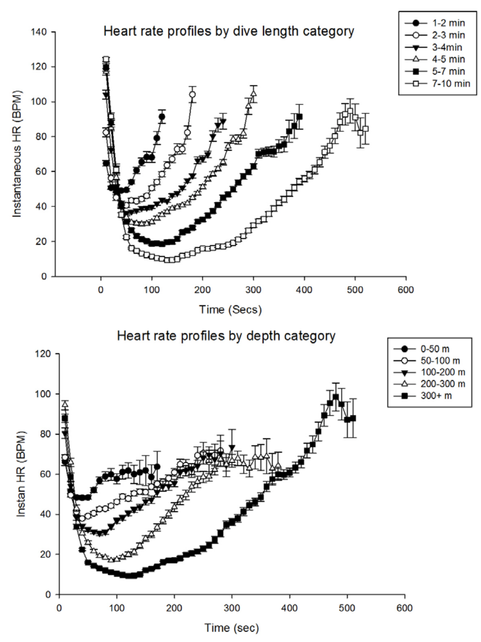

Figure 2. Instantaneous heart rate in 30-sec intervals in dives of different duration and depth categories. Initial heart rates are progressively higher for deeper dives of longer duration, and the degree of bradycardia increases with maximum depth and duration of dives.

IMPACT/APPLICATIONS

In prior ONR-funded research, partial pressure of oxygen (P_{O2}) profiles provided evidence that lung collapse occurred near 200-m depth in diving sea lions (McDonald and Ponganis 2012). This impairment of gas exchange limits nitrogen uptake at depth and preserves lung oxygen for later use during ascent. Now, this more recent research has revealed that heart rate rapidly declines during descent of deep dives to values less than 10 beats min^{-1} (Fig.1). Such a low heart rate also limits the absorption and distribution of both nitrogen and oxygen at depth (through reductions in pulmonary and aortic blood flow). As a result of these physiological processes, the sea lion can maintain arterial hemoglobin saturation above 90% during deep dives as long as 7 minutes (McDonald and Ponganis 2012; McDonald and Ponganis 2013). In contrast, the elephant seal (*Mirounga angustirostris*), which dives on expiration and has less than 5% of total body O_2 stores in the respiratory system, experiences significant hypoxemia with routine arterial hemoglobin desaturation to 10 to 20% (Meir et al. 2009). However, similar to the sea lion, the emperor penguin (*Aptenodytes forsteri*), another animal that dives on inspiration with a large respiratory O_2 store, also can maintain arterial saturations during dives as long as 10 min (Meir and Ponganis 2009). It is also notable that a severe bradycardia during descent occurs in deep-diving emperor penguins (Ponganis, unpublished data), and in deep-diving bottlenose dolphins (*Tursiops truncatus*), which also dive on inspiration (Houser et al. 2010; Williams et al. 1999). For these reasons, it is hypothesized that the heart rate profile during deep dives of California sea lions is universal among higher vertebrates that dive on inspiration. Hence, both lung collapse and the heart rate profile make the California sea lion a valuable model to investigate physiological responses and gas uptake / distribution during deep dives.

The lower heart rates during deeper, longer dives observed in this study and the lack of blood oxygen depletion during these deep dives that were documented in our prior ONR study (McDonald and Ponganis 2012; McDonald and Ponganis 2013) also have implications for the management of oxygen stores and the physiological basis of the ADL. The concept that most dives are aerobic in nature and do not exceed an aerobic dive limit (ADL - dive duration associated with the onset of post-dive blood lactate accumulation) has dominated the interpretation of dive behavior and foraging ecology over the past 30 years (Costa et al. 2001; Kooyman et al. 1980). However, because of technical difficulties, the ADL has rarely been measured. Instead, researchers have had to resort to estimations of total O_2 store depletion, i.e., calculated ADLs (cADLs) (Costa et al. 2001; Weise and Costa 2007). Our findings in sea lions support the concept that the physiological basis of the ADL is muscle oxygen depletion and subsequent glycolysis. The lung and blood oxygen stores are not completely depleted in even the longest of sea lion dives. The severe bradycardia during deep dives contributes to the preservation of the blood and lung oxygen for use during ascent, and it also creates greater reliance of muscle metabolism on the myoglobin-bound muscle oxygen store. In addition, the lack of correlation between heart rate and stroke rate in Fig. 1 suggests that muscle blood flow and oxygen delivery are not coupled with stroke effort. These findings reinforce our hypothesis that depletion of the muscle oxygen store with subsequent glycolysis underlies the ADL.

RELATED PROJECTS

This project is building on our findings from our previous ONR funded project “Blood oxygen depletion in California sea lions: How close to the limit?” (award #: N000141010514)

REFERENCES

Costa, D.P., N.J. Gales and M.E. Goebel. 2001. Aerobic dive limit: how often does it occur in nature? Comparative Biochemistry and Physiology A 129: 771-783.

Houser, D.S., L.A. Dankiewicz-Talmadge, T.K. Stockard and P.J. Ponganis. 2010. Investigation of the potential for vascular bubble formation in a repetitively diving dolphin. J Exp Biol 213: 52-62.

Kooyman, G.L., E.A. Wahrenbrock, M.A. Castellini, R.W. Davis and E.E. Sinnett. 1980. Aerobic and anaerobic metabolism during diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. Journal of Comparative Physiology 138: 335-346.

McDonald, B.I., and P.J. Ponganis. 2012. Lung collapse in the diving sea lion: hold the nitrogen and save the oxygen. Biology Letters 8: 1047-1049.

McDonald, B.I., and P.J. Ponganis. 2013. Insights from venous oxygen profiles: oxygen utilization and management in diving California sea lions. Journal of Experimental Biology 216: 3332-3341.

Meir, J.U., C.D. Champagne, D.P. Costa, C.L. Williams and P.J. Ponganis. 2009. Extreme hypoxemic tolerance and blood oxygen depletion in diving elephant seals. Am J Physiol Regul Integr Comp Physiol 297: R927-939.

Meir, J.U., and P.J. Ponganis. 2009. High-affinity hemoglobin and blood oxygen saturation in diving emperor penguins. Journal of Experimental Biology 212: 3330-3338.

Ponganis, P.J., G.L. Kooyman, L.N. Starke, C.A. Kooyman and T.G. Kooyman. 1997. Post-dive blood lactate concentrations in emperor penguins, Aptenodytes forsteri. Journal of Experimental Biology 200: 1623-1626.

Weise, M.J., and D.P. Costa. 2007. Total body oxygen stores and physiological diving capacity of California sea lions as a function of sex and age. Journal of Experimental Biology 210: 278-289.

Williams, T.M., J.E. Haun and W.A. Friedl. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). I. Balancing the demands of exercise for energy conservation at depth. Journal of Experimental Biology 202: 2739-2748.